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# Colour-space distortion in women who are heterozygous for colour deficiency

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ABSTRACT

We examined colour perception among a group of women heterozygous for colour vision deficiency. Judgements of colour dissimilarity were collected by presenting colour stimuli in groups of three for odd-one-out decisions. The judgements were summarised as one consensus colour space for the heterozygotes and another for age-matched controls. Individual differences MDS was also applied, resulting in a single colour space which can be adjusted to fit each subject's responses individually by compressing it along its axes. Heterozygous women showed a trend towards colour-space compression in a red–green dimension, or reduced salience of that dimension compared to controls, though less extreme than found in overt colour deficiency.



## 1. Introduction

About 15% of women are heterozygous for some form of colour vision deficiency (CVD). That is, they possess a genetic abnormality on one of their two X chromosomes, affecting the photopigments (opsins) which subserve colour vision. The retina of a heterozygous woman is a mosaic in which some cone cells express the aberrant gene while others express the normal copy, depending on which X chromosome is active (inactivation of one X chromosome occurs randomly in retinal stem-cells at some stage of fetal development). The normal cells are sufficient to provide full trichromatic vision. Thus heterozygotes are carriers of the CVD, with a 50% chance of passing on the trait to a child. In particular, the single X chromosome of a CVD male is necessarily inherited from his mother and passed on to his daughter, making them carriers, while his sister has a 50% chance of inheriting the affecting gene.

The two common forms of congenital CVD are protan and deutan defects, involving the long-wavelength-sensitive and medium-wavelength-sensitive opsins respectively (L-opsin and M-opsin). A second classification further divides this dichotomy by distinguishing between dichromacy and anomalous trichromacy. Thus there are two forms of dichromacy, protanopia and deuteranopia, in which the L- or M-opsin, respectively, is thought to be missing or replaced with the other, so the retina contains only one of the two cone types. The corresponding forms of anomalous trichromacy are protanomaly and deuteranomaly. Both are marked by a reduced difference between the L- and M-cones in the wavelengths they absorb, because the absorption spectrum of the L-opsin is shifted towards the M-opsin, or vice versa. According to the spectral proximity hypothesis (Regan, Reffin, & Mollon, 1994), a smaller difference between absorption spectra results in a more severe deficit.

Women heterozygous for CVD are not obviously colour-deficient, and do not stand out from normal controls in terms of their anomaloscope mid-point matches (Feig & Ropers, 1978). However, their individual ranges of acceptable matches are on average wider than normal (Lang & Good, 2001), indicating that the reduced population of normal L- or M-cones is not enough to provide the normal level of colour discrimination along the red–green continuum. Further evidence that hue discrimination is lower among carriers comes from their higher error scores on the FM100-Hue test (Krill & Schneiderman, 1964; Verriest, 1974) and on the D15-DS test (Lang & Good, 2001). It is also known that when a white or yellow background is modulated by adding a subtle red–green grating (Hood, Mollon, Purves, & Jordan, 2006; Lang & Good, 2001), the modulation is harder for deutan carriers to detect (but not protan carriers), though individual carriers may fall within the range of normal variation (Wieland, 1933). Note that these subtle departures from normal trichromatic colour vision generally involve barely-discriminable colour differences at the threshold of detection.

Finally, the reduced signal from L- or M-cones also impacts on luminance-channel processing. Thus carriers of protanopia are characterised by "Schmidt's sign", their reduced sensitivity to long-wavelength light (Schmidt, 1934). Crone (1959) found a corresponding insensitivity to mid-wavelength lights among deutan carriers. Both observations have been replicated by Hood et al. (2006) and Jordan and Mollon (1997).

These psychophysical results lead one to wonder whether these systematic discrepancies between heterozygotes and normal

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controls extend to the experiential level of subjective dissimilarity. To this end we examine judgements of large dissimilarities between clearly-distinct pairs of colours. Colour-deficient observers certainly differ from controls at this subjective level, in that they experience a smaller dissimilarity between red and green hues; one could say that their personal maps of the colour space are compressed along their axis of confusion (Farnsworth, 1943). Personal colour spaces also vary among normal observers. Moreover, closely-related observers have more similar colour spaces than unrelated individuals, presumably reflecting some genetic contribution to the individual variations (which may or may not be linked to the X chromosome). More specifically, pairs of genetically-identical (monozygous) twins prove to have more similar spaces than pairs of fraternal (dizygous) twins, and both groups are on average more similar than unrelated pairs (Bimler & Kirkland, 2004a; Paramei, Bimler, & Mislavskaia, 2004).

Following previous studies (e.g. Bimler, Kirkland, & Jameson, 2004) we use the method of triads to elicit dissimilarity judgements. Subjects view combinations of three colour samples (triads) and within each triad they select the odd-one-out sample (least-similar to the other two). This is equivalent to the assertion that one sample pair is more similar than the other two pairs. Thus, the data are not ratio-level or interval-level estimates of the dissimilarities for various pairs, but rather are ordinal-level rankings of pairwise similarities.

Such data can be analysed in several ways. One approach attempts to reconstruct and then to compare collective colour spaces for specific groups of observers. This relies on "colour space" as a geometrical metaphor in which each stimulus is represented by a point, and the data are treated as statements about the relative distances between pairs of points. There is a long tradition of applying this approach to colour vision (reviewed by Indow, 1988). The present data do not permit the reconstruction of an individual space for each observer. However, we can assume that each observer's space is a distorted variant of a single collective space, while defining the nature and the parameters of the allowable variation; each subject's responses can then be summarised by calculating his or her values of the relevant parameters. The distribution of these parameters reveals whether the heterozygotes belong to the distribution of normal controls (NCs), or whether they are more like CVD observers.

The second approach does not invoke the geometrical metaphor. Instead we calculate the concordance between each pair of observers, i.e. the fraction of triads for which they chose the same colour as odd-one-out. The structure of the matrix of concordances then reveals whether heterozygotes experience the colour world in the same way as NCs, or whether they share some of the characteristics of CVDs.

## 2. Method

### 2.1. Stimuli

A Xerox DocuColor 6060 laser printer was used to print triads of colour samples on cards 4 cm square, with identifying numbers, as shown in Fig. 1. The hues comprising each triad were printed as 12-mm circles surrounded by 1-mm black outlines (the same size as the caps used in the D15 panel test), arranged as an equilateral triangle against a neutral background, Munsell N/6. The specifications of stimuli (i.e. their components of cyan, magenta, yellow and black pigments) were fine-tuned until the authors could not distinguish them from Munsell paper originals. We prepared a primary list and a secondary list, each consisting of 75 unique triads.

The 16 stimuli were based on the colours used in the D15 panel test for colour vision, which have featured in previous research

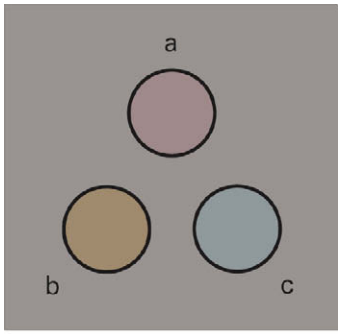


**Fig. 1.** Example of printed triad cards.

(Bimler & Kirkland, 2004a, 2004b; Bimler et al., 2004; Feitosa-Santana et al., 2006). They form an incomplete circle in the colour plane, as shown in Fig. 2, which locates them using CIELAB coordinates. In the third dimension of colour space (lightness) they occupy two parallel planes. Ten stimuli matched the Munsell specifications of the D15 caps, with the same lightness and saturation (value = 5 and chroma = 4) and Hue coordinates ranging at roughly equal intervals from blue around the hue circle to purple. The other six stimuli, with hues of 10B, 5BG, 10GY, 10YR, 2.5 R and 5 P, were lighter and less saturated than their D15 equivalents (value = 6.5 and chroma = 3).

With 16 stimuli, 560 different triadic combinations are possible, in which a given pair of stimuli appears 14 times (in combination with the other 14 stimuli). In the subset of 150 triads comprising the two lists, the various pairs of stimuli appeared in from 1 to 6 triads (around a mean of 3.75). Each stimulus appeared from 26 to 30 times.

### 2.2. Procedure

Subjects viewed these cards in random order, in each case deciding on the least-similar stimulus. Their responses were re-

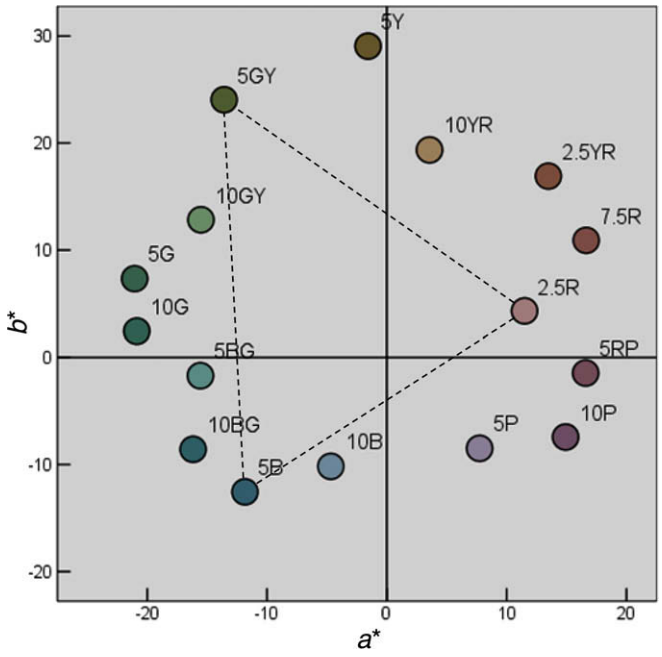


**Fig. 2.** Locations of the 16 stimuli in the colour plane, with the CIELAB coordinates $a^*$ and $b^*$ as axes. Triangle indicates a triad where the choice of least-similar stimulus is sensitive to axial compression.

corded as 'a', 'b' or 'c'. If they could not immediately decide for a problematic triad, they could set it aside and revisit it later. The numbers identifying particularly difficult choices were also recorded. After the session, the cards were shuffled into a random order for the next subject.

For most sessions the cards were viewed resting on a sheet of grey card (N5), within a desk-top booth of walls and baseboard painted matt grey. Daylight-quality illumination was provided by Philips 'TL'D/950 fluorescent tubes (colour temperature 5300 K, colour rendering index > 95). The tubes were raised or lowered to maintain a desk-top luminance level of 500 lux, as measured with a photometer. Experimenter and subject both wore disposable white gloves to avoid colour-contrast effects. A small number of sessions were carried out in bright indirect sunlight, at the homes of subjects who were unable to travel.

No time constraint was imposed, and subjects were encouraged to take breaks to avoid fatiguing their eyes or falling into routine responses. All subjects responded to the primary list and most also responded to the secondary. Both lists together took 10–30 min.

### 2.3. Subjects

Thirty-one male subjects recalled having once failed a Lantern or Ishihara test. This self-assignment to the CVD group was confirmed in each case by their performance on the D15 or D15–DS panel tests.

Of these 31 subjects, 14 were severely colour-deficient according to their patterns of triad responses, as analysed below. It is convenient to label these cases as D for Dichromats (though they may also contain 'extreme anomalous trichromats'). The other 17 cases were moderately colour-deficient, and are labelled here as AT for Anomalous Trichromats. The former group were further divided into six protanopes and eight deuteranopes, on the basis of their pattern of errors on the panel test results. The latter group were subdivided into 12 protanomals and five deuteranomals.

Data were collected from family members of some but not all CVDs. These included 11 mothers and daughters of severe cases (eight of protanopes and three of deuteranopes), and nine of moderate cases (four of protanomals and five of deuteranomals). In theory these 20 women were heterozygous for colour deficiency. Another nine women were sisters of CVDs, and were presumed to have a 50% chance of heterozygosity. Ten fathers and sons of CVD subjects also volunteered for the study. There is no reason to expect them to show colour deficiency.

Finally, 49 subjects reported themselves as having normal colour vision, and confirmed this by passing the D15 and D15–DS tests. The numbers of male and female controls were balanced. It was not practical to match the ages of the CVD, heterozygote and control groups, because of the different generations involved.

These subjects were initially recruited through advertising on University noticeboards, and by calling upon social contacts. Word-of-mouth transmission brought in further subjects.

### 2.4. Analysis

Using the index $m$ to identify subjects, for each subject we calculate a 16-by-16 matrix $C_m$ of estimated inter-stimulus similarities. Each element of $C_m$ ($c_{mij}$) is the fraction of triads containing the $i$th and $j$th stimuli in which the subject chose that pair as most similar. For a given pair of subjects ($m$ and $n$), we now calculate $r_{mn}$ – the binomial correlation between $c_{mij}$ and $c_{nij}$, over the 120 stimulus pairs $i < j$.

Cultural consensus analysis or CCA (Moore, Romney, & Hsia, 2002) sets out some criteria for the matrix of $r_{mn}$ values: if they are met, we can assume that an underlying consensus exists about the 'correct responses', shared across the population. Some subjects have better access to this consensus than others; they are more competent observers or reporters. This 'competence' or 'accuracy' is quantified by the $m$th subject's loading on F1: the first principal component to emerge when Principal Components Analysis or PCA is used to decompose the $r_{mn}$ matrix. Other principal components represent distinct forms of disagreement among the subjects.

If the evidence points to the existence of group differences, it remains to identify their nature. The data reveal more when they are analysed in the context of a geometrical framework – that is, a 'map' of colour space, in which a separate point represents each stimulus, and points are arranged so that the distances between them replicate the dissimilarities perceived among stimuli. Farnsworth (1943) showed that as well as accounting for normal perceptions, a consensus colour space can accommodate the colour confusions of CVDs, by compressing it along some axis so as to reduce the distances (and dissimilarities) between easily-confused colours, such as reds and greens. The extent of compression is an index of the severity of the deficit, while the angle of compression (the 'axis of confusion') distinguishes protans and deutans.

Following Farnsworth's insight, numerous researchers have used multidimensional scaling (MDS) to quantify individual variations in colour perception (Cavonius, Müller, & Mollon, 1990; Chang & Carroll, 1980; Offenbach, 1980; Shepard & Cooper, 1992; Stalmeier & de Weert, 1991). This is part of a larger research tradition where models of colour space are obtained from judgements of similarity by analysing them with MDS (Indow, 1988). Typically the "weighted Euclidean" framework of individual difference is applied, which ignores the protan/deutan distinction, and assumes that any dilation or compression of colour space takes place along the same axes for all observers – including along a third 'lightness' axis, if the stimuli vary in luminance (Wish & Carroll, 1974).

That framework is used here, but we also apply the "idiosyncratic weights" framework (Bimler et al., 2004; Carroll & Wish, 1974; Paramei, Bimler, & Cavonius, 2001), where subject-specific parameters include the angle as well as the extent of compression. For some triads, the angle of compression of colour space affects the predicted odd-one-out judgement, as illustrated in Fig. 3, using the locations of the stimuli in CIELAB space.

CIELAB or several other standard colour-appearance models would also have served as the undistorted consensus colour space, used to reconstruct the compression-angle parameter from each subject's actual judgements. Here we obtain it by applying MDS to the pooled data from NCs, so that the outcome is not reliant on stimuli matching their intended Munsell specifications. More specifically, the data were analysed with MTRIAD, an algorithm that maximises the fit between the reconstructed map distances and the observed triadic responses (Bimler, Kirkland, & Jacobs, 2000). Similar algorithms are TRISOSCAL (Coxon & Jones, 1979, Appendix T3.1.1) and MAXSCAL (Takane, 1978).

## 3. Results

The unrotated PCA solution revealed that a significant number of participants had small or negative loadings on the first component. The mean loading (i.e. the average level of competence) was quite low, at 0.56. Accordingly, we abandoned the assumption of a single underlying consensus, and opted for a two factor solution (Fig. 4). There being no reason to believe that the factors would be orthogonal, the Oblimin criterion was used for rotation. The two factors between them account for 43% of total variance; a case could be made for including a third factor, which would account for an additional 4%, but this would complicate the interpretation.

The crucial aspect of the PCA solution is that high loadings on F2 were only found for CVD males. Below, we will divide the CVD sub-

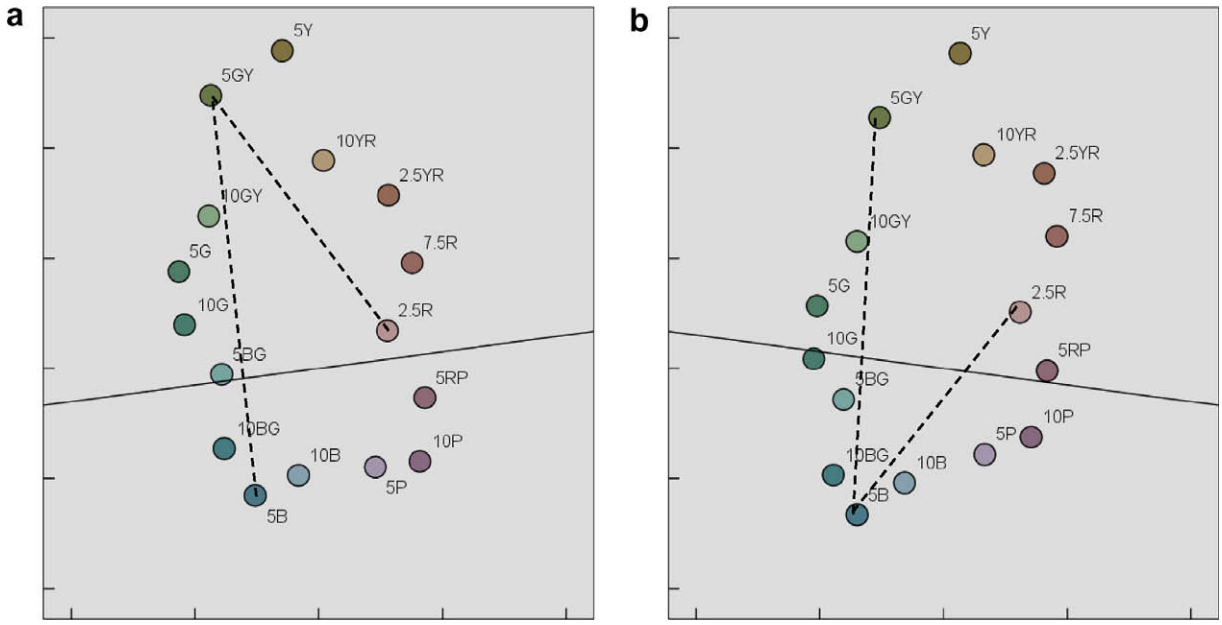


**Fig. 3.** Compressing colour space along (a) a 'protan axis' or (b) a 'deutan axis' shrinks distances or dissimilarities between stimuli. Axes are linear combinations of the CIELAB coordinates $a^*$ and $b^*$. Compression along the two directions leads to different predictions of odd-one-out judgements: in the example triad, 5GY or 5B becomes the apex of the triangle.

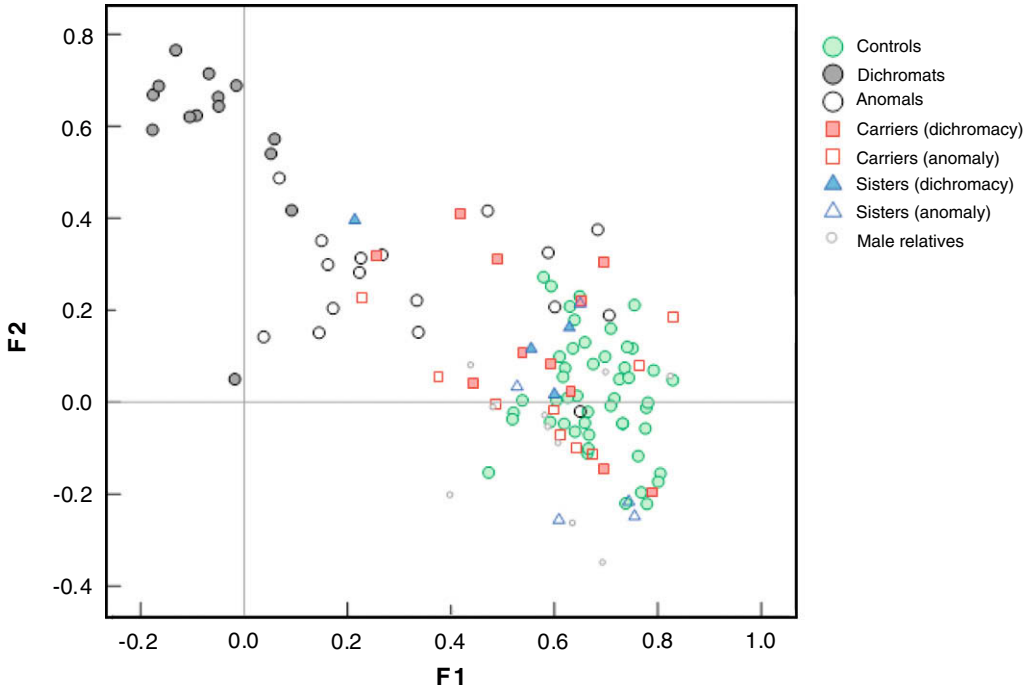


**Fig. 4.** Factor loadings of subjects in rotated PCA solution. Perceived dissimilarities for normal observers and dichromats are dominated by principal components F1 and F2, respectively.

jects into two groups, Dichromats and Anomalous Trichromats (ATs). Both groups depart significantly from the NC population, tending to load higher on F2 and lower on F1 (Table 1). Two corresponding groups of putative heterozygous females can also be defined: carriers of Dichromacy, and carriers of Anomalous Trichromacy. The former group also departs significantly from the controls.

We applied the methods of CCA to each group separately, and found more agreement within them than among the subjects as a whole. The PCA solution for each group was dominated by a single component: that is, it is valid to speak of a consensus specific to the NCs, another to the dichromats, and so on (with considerable overlap between them). Subjects show considerably more competence when judged in terms of agreement with the appropriate group consensus (Table 1 also lists mean values for each group). The consensus for the NCs' data is almost identical to F1 from the combined PCA solution of Fig. 4 ($r = 0.987$).

**Table 1**
Distributions of factor loadings for CVD males and heterozygous females, compared to the distribution for NT controls. When two *p*-values are given, they are the significance of the difference with and without the assumption that the two distributions have the same variance. Final row lists the mean competence of each group (i.e. mean loading on first factor of a PCA solution for that group's data in isolation).

| | 49 Controls | 14 Dichromats | 17 ATs | 11 D carriers | 9 AT carriers |
|---|---|---|---|---|---|
| F1 loading (mean ± s.e) | 0.681 ± 0.012 | −0.060 ± 0.023<br>$p < 0.0001$ | 0.343 ± 0.055<br>$p < 0.0001$ | 0.564 ± 0.046<br>$p = 0.001/0.032$ | 0.579 ± 0.063<br>$p = 0.010/0.148$ |
| F2 loading (mean ± s.e) | 0.016 ± 0.017 | 0.589 ± 0.047<br>$p < 0.0001$ | 0.260 ± 0.030<br>$p < 0.0001$ | 0.134 ± 0.060<br>$p = 0.013/0.081$ | 0.027 ± 0.040<br>n.s. |
| Mean competence | 0.65 | 0.62 | 0.51 | 0.65 | 0.65 |

The control group does not separate males and females. A small male/female difference is sometimes observed (e.g. Bimler et al., 2004), but was not visible here. Comparing the Dichromacy carriers with female controls only, the mean values of F1 and F2 are still different, though the significance falls to $p = 0.05$ and 0.02, respectively. We cannot exclude the possibility that some of the 23 female controls were themselves heterozygous for a colour deficiency, but it is hard to imagine that this would materially affect the results.

In this analysis, the rotated factors are simply two idealised patterns of inter-item dissimilarities – two "points of view" (Tucker & Messick, 1963) – which are combined in various proportions to produce the various observers' personal colour spaces. These patterns can be summarised by converting them back into 16-by-16 matrices for treatment with non-metric MDS (Kruskal's algorithm, implemented in Proxscal software). Fig. 5 shows the two points of view. For the sake of clarity, we obtained two-dimensional rather than three-dimensional solutions. Note that the two dimensions of Fig. 5a between them represent the latent structure of F1, and the two dimensions of Fig. 5b represent the structure of F2; that is, the dimensions do not correspond to the principal components.

These colour spaces are gratifyingly close to those obtained in an earlier application of points of view analysis to colour vision data (Helm & Tucker, 1962). In both cases, the vertical axis is a Blue–Yellow gradient. The horizontal axis is an opposition between Green and Red stimuli in Fig. 5a, but in Fig. 5b it is not readily interpretable. F1 – the point of view shared among NCs – reduces to a reconstruction of the colour circle. This contrasts with F2, which dominates the responses of the CVDs, in which the green–red axis has almost vanished.

A more accurate reconstruction of the arrangement of stimuli in colour-space (as in Fig. 2) can be achieved by applying MDS directly to the triadic data. In Fig. 6a, b and c, the stimulus locations have been optimised to match the data from NCs, dichromats, and putative dichromacy heterozygotes, respectively. Relative to Fig. 6a, 6b is compressed along the horizontal (green–red) axis, to the extent that red and green stimuli are adjacent (i.e. indistinguishable), while the sequence of stimuli along the vertical axis (blue–yellow) is unchanged. The key feature of Fig. 6c is its *mild* compression along a green–red direction. The dispersal of points along the horizontal axis accounts for 52% of the total variance in Fig. 6a, falling to 46% in Fig. 6c. Conversely, the vertical axis accounts for 42% of variance in Fig. 6a and 44% in Fig. 6c. There is a third dimension, not shown here, separating the lighter and darker stimuli, which accounts for 6% and 10%, respectively.

It remains to quantify this compression for individual subjects as well as for groups. For this purpose, the combined NC solution of Fig. 6a is distorted for each subject so that the modified distances among stimulus-points are the best possible match to that subject's dissimilarity judgements. The distortion is parameterised by the variables $\theta_m$, the angle of a compression axis ($-90° < \theta_m \leqslant 90°$); $w_{m1}$, the salience (i.e. the contribution to distance) of inter-point separation measured along this axis; and $w_{m2}$, the salience of separation perpendicular to the axis. There is also a third axis, Lightness, with a corresponding salience parameter $w_{m3}$, but this can be ignored here. The salience

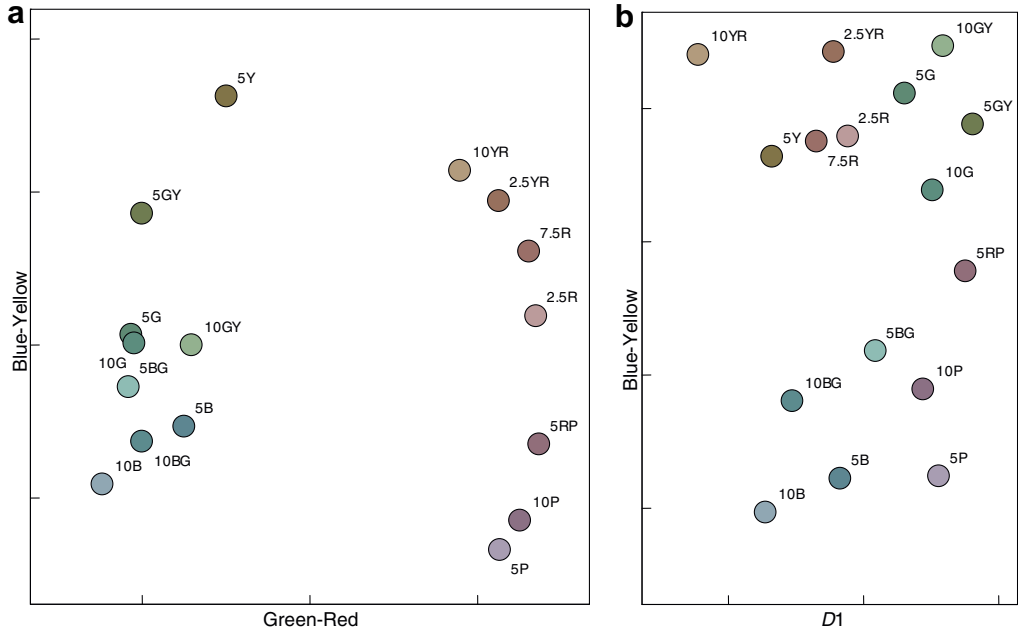


**Fig. 5.** Two-dimensional MDS solutions representing the internal structure of principal components (a) F1 and (b) F2 from rotated PCA solution.

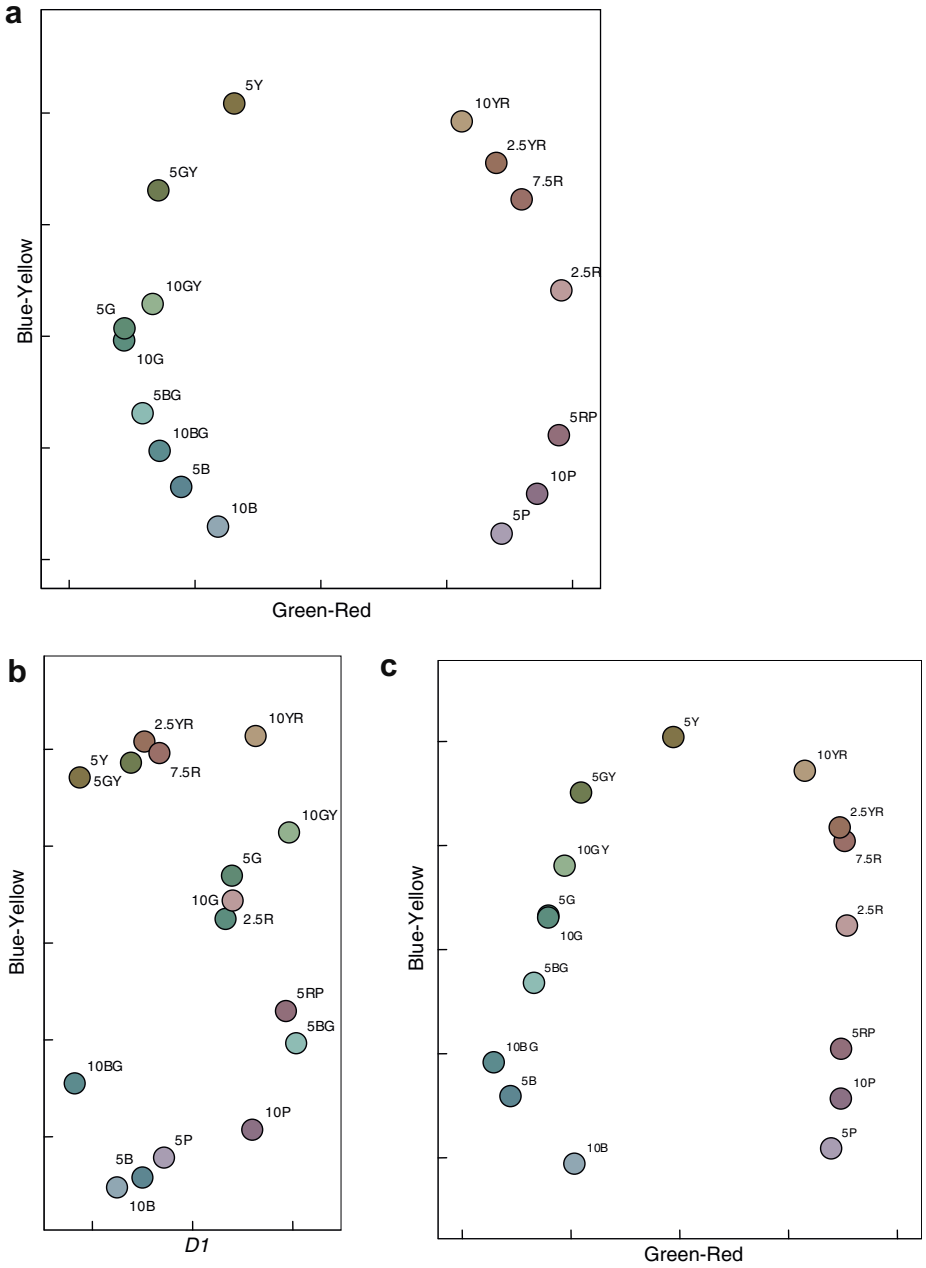


**Fig. 6.** First two dimensions of separate maximum-likelihood MDS solutions for (a) 49 controls; (b) 19 dichromats, and (c) 11 dichromat carriers, showing compression of colour space in a green–red direction for dichromats, and also in a milder form for carriers. Units are arbitrary.

parameters can conveniently be reduced to the value $r_m = (w_{m2}^2 - w_{m1}^2)/(w_{m2}^2 + w_{m1}^2)$, where $0 \leqslant r_m \leqslant 1$. The extremes of $r_m$ correspond to the cases of no compression at all, and complete compression of the colour plane to a line.

In Fig. 7a and b, these parameters are plotted as polar coordinates, using $r_m$ as the radial coordinate and $2\theta_m$ as the angular coordinate, where each point characterises one subject. Normal controls are concentrated near the centre of these diagrams. Closer to the perimeter, each male CVD subject was assigned to the AT group (moderate deficiency) if $r_m \leqslant 0.9$, or to the D subgroup (severe deficiency) if $r_m > 0.9$. Notice that $\theta_m > 0$ for all protans, and $\theta_m < 0$ for almost all deutans. This confirms an earlier result from a study where the protan/deutan differential diagnosis could be checked by anomaloscope readings (Bimler et al., 2000). The points representing Dichromacy carriers in Fig. 7a are not centred on the centre of the diagram – that is, they tend to show colour-space compression along one particular axis – although they overlap with the distribution of NCs.

For subjects who completed both the primary and secondary triad list, we obtained separate parameters for each list. These are plotted in Fig. 8. Distances between points for the two lists are small compared with distances between two points at random. Thus, the parameters which characterise a subject's responses are reasonably stable and replicable.

## 4. Discussion

Before continuing, we should note that the framework of colour-space compression used here for individual differences is only an approximation. It is adequate for Munsell papers, which have broad reflectance spectra, but it does not accommodate the possi-

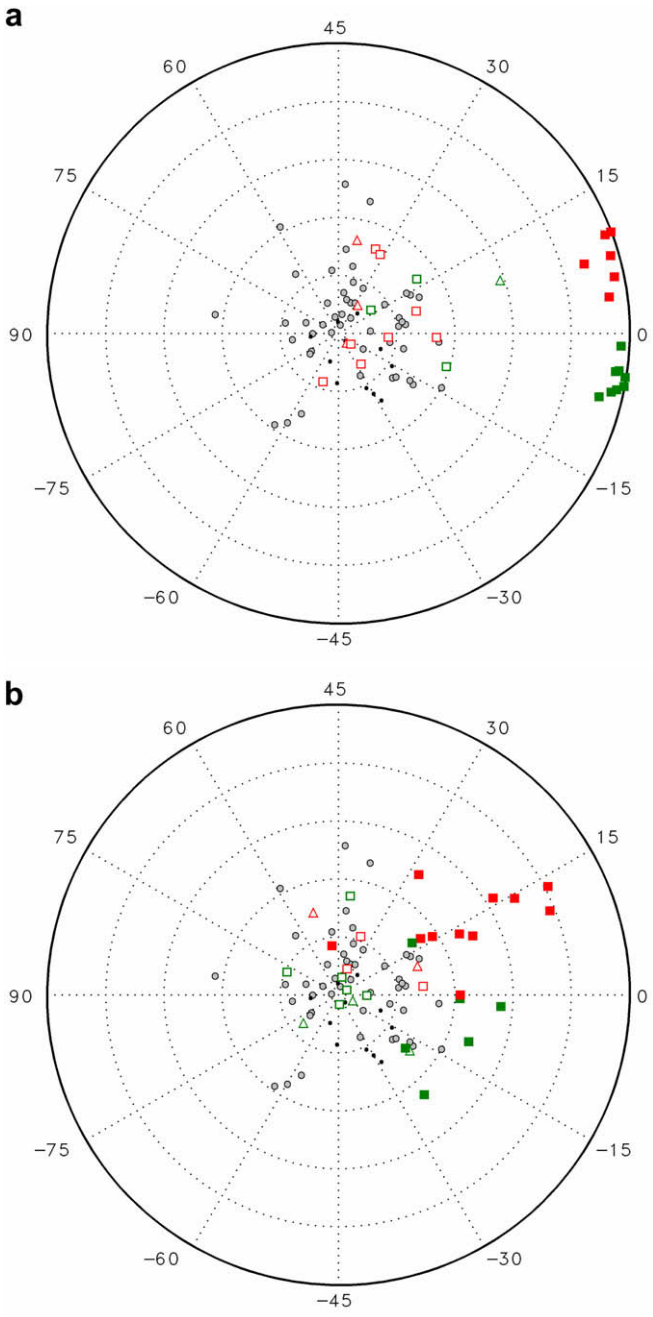


**Fig. 7.** Subjects' colour-space compression parameters, plotted in radial coordinates, where red and green symbols indicate protan and deutan deficiency. Grey circles indicate normal controls; small black dots are sons and fathers of CVD subjects: (a) 14 dichromats (solid squares); 11 mothers and daughters (open squares); four sisters (open triangles) and (b). 17 anomalous trichromats (solid squares); nine mothers and daughters (open squares); five sisters (open triangles).

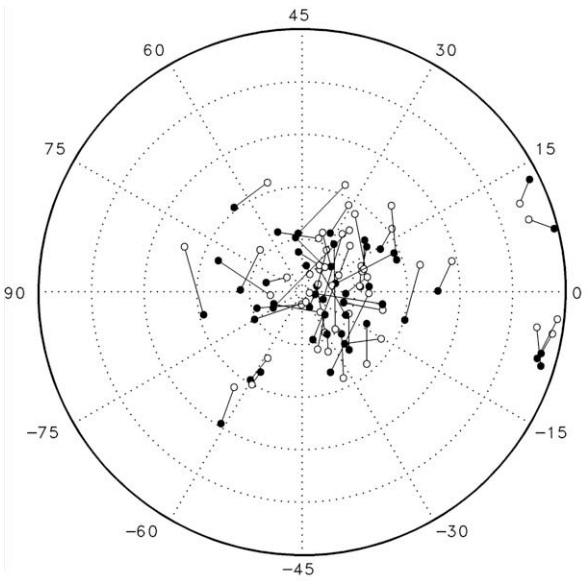


**Fig. 8.** Separate colour-space compression parameters for the two triad lists. Each pair of solid and open circles (connected by a line) represents a subject's values for the primary and secondary list.

bility of stimuli that vary in ways that are apparent to a protanope (for instance) but not to a normal trichromat. Bosten, Robinson, Jordan, and Mollon (2005) created such stimuli from pigments with sharp-peaked reflectance spectra. The spectra of the present laser-printed stimuli have not been measured, but the similarity judgements from CVDs and heterozygotes seem to be compatible with the approximation (Figs. 5b and 6b and c).

Previous research with the methodology of psychophysics has revealed that women who are heterozygous for colour deficiency, i.e. who carry a single copy of an aberrant gene for the L- or M-photopigment, incur a slight reduction of colour discrimination. According to the present results, the effects extend to the subjective realm, so that heterozygotes experience the world in a slightly different way from normal trichromats. More specifically, when heterozygotes assess the subjective dissimilarities among hues, they see hue pairs that differ along a green–red direction in colour space as slightly less dissimilar than normal.

Several situations can be distinguished here. First, it may be that one copy of the gene for the L- or M-photopigment is absent or non-functioning. This trait expresses as dichromacy when inherited by a male, whose retina produces no L-M signal to detect the green–red differences among hues. A second possibility is that the absorption spectrum of the L-pigment has been shifted and almost coincides with that of the M-pigment (or vice versa), causing a much-weakened L-M signal in the affected male, and making him an EAT or extreme anomalous trichromat. In both cases, the female carrier will possess fewer than usual L-cones (or M-cones), reducing the strength of the L–M signal; in the second case, her retina will also contain a population of cells that behave more like M-cones (or L-cones). For our purposes, it was enough to select the severely deficient male observers, without making a finer distinction between dichromats and EATs (which would require at least an anomaloscope measurement, and preferably a genotype). Their mothers and daughters, heterozygous for the various genetic aberrations involved, differed significantly from normals (Fig. 6a) – that is, any post-receptor mechanisms in their visual processing that might correct for the weakened (L–M) signal was not able to compensate entirely. Even so, the heterozygotes overlapped with the normal range, and their collective colour space was less distorted than that seen in clinical colour deficiency.

It is possible that some of the CVD males we assigned to the dichromat group were in fact ATs. Definitive diagnoses as D or AT with an anomaloscope would have been preferable, but these were not available. However, any mistake would only have reduced the difference between dichromacy carriers and NTs by diluting the former group with AT carriers.

Lang and Good (2001) found that colour discrimination was only reduced in women heterozygous for deuteranopia; protanopic heterozygotes did not differ from controls. Hood et al. (2006) ascribed this to the fact that a normal retina contains twice as many

L-cones as M-cones, so that the former are merely reduced to equal proportions in the retinal mosaic of a protanopic carrier, whereas for a deuteranopic carrier they come to outnumber M-cones in a 5:1 ratio. The present study involved too few subjects to examine protanopic and deuteranopic carriers separately, but the former dominate the group of dichromacy carriers, while both sub-groups seem to be equally displaced from normality in Fig. 7a. This contrast with Hood et al. suggests the tentative conclusion that colour dissimilarities are not linked to the heterozygous genotype in the same way as discrimination.

A third situation, accounting for male subjects who express moderate protanomaly (or deuteranomaly), is where the absorption spectrum of the L-pigment (or M-pigment) has been shifted to somewhere between that of the normal pigments, reducing but not vitiating the contrast with its counterpart. To be specific, let us call the intermediate photopigment L*. Heterozygous females, possessing one copy each of the aberrant gene and the normal version, express a mixture of L- and L*-cones. They showed a reduction in salience of the green–red colour axis, but here the difference from controls was not significant.

Several authors have pointed out that the four distinct populations of cone cells in the retinae of such heterozygotes, rather than three, might capture additional colour information (Jameson, Highnote, & Wasserman, 2001; Jordan & Mollon, 1993). If the centre/surround difference cells in the retina take advantage of this information and pass it on to subsequent stages of visual processing – creating (L–L*) and (L*–M) signals in addition to (L–M) – then heterozygous women could in theory distinguish among combinations of light that appear identical to a normal observer (also Bosten et al., 2005). If it actually exists, this phenomenon of 'functional tetrachromacy' does not conflict with the evidence that heterozygosity is associated with reduced discrimination among closely-related hues.

The X-linked nature of inherited CVDs predicts that the sons and fathers of CVD males should be normal. The distribution of such male relatives (when their responses are reduced to $r_m$, $\theta_m$ parameters) is consistent with the prediction, though more subjects are needed before we can assert that it is the same as the distribution of normal controls.

The X-linked inheritance pattern also predicts that the sisters of CVD males have an equal chance of being normal or heterozygous. In theory, then, if we collected data from sufficiently many sisters of dichromats, we would observe two populations of $r_m$, $\theta_m$ parameters, overlapping to form an elongated distribution in a polar coordinate diagram (see the points in Fig. 7b). Again, more subjects are required to confirm this. Finally, we note that in any extension of the study, with a greater number of subjects, their task could simplified by using only those triads which prove to discriminate among subject sub-groups.

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